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The Leaf Spots of the Elm

THE LEAF SPOTS OF THE ELM

BY

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I HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER MY
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THE LEAF SPOTS OF THE ELM

I. INTRODUCTION.

Of the genus *Ulmus* about eighteen species are known, (2) widely distributed throughout the cold and temperate regions of the northern hemisphere. Six of these species, *Ulmus americana*, *U. fulva*, *U. racemosa*, *U. alata*, *U. serotina*, and *U. crassifolia*, are native to America and occur naturally from Labrador to southern Mexico. None, however, occurs west of the Rocky Mountains. *Ulmus alata*, *U. crassifolia*, and *U. serotina* are tender and do not grow well in the northern states. They are quite extensively used for lawn and avenue trees in the south. *Ulmus americana*, the most widely distributed American species, occurs in practically every state east of the Rocky Mountains and in Canada. It is the most characteristic tree of the northeastern states, and is very widely used for street planting and as an ornamental tree for lawns.

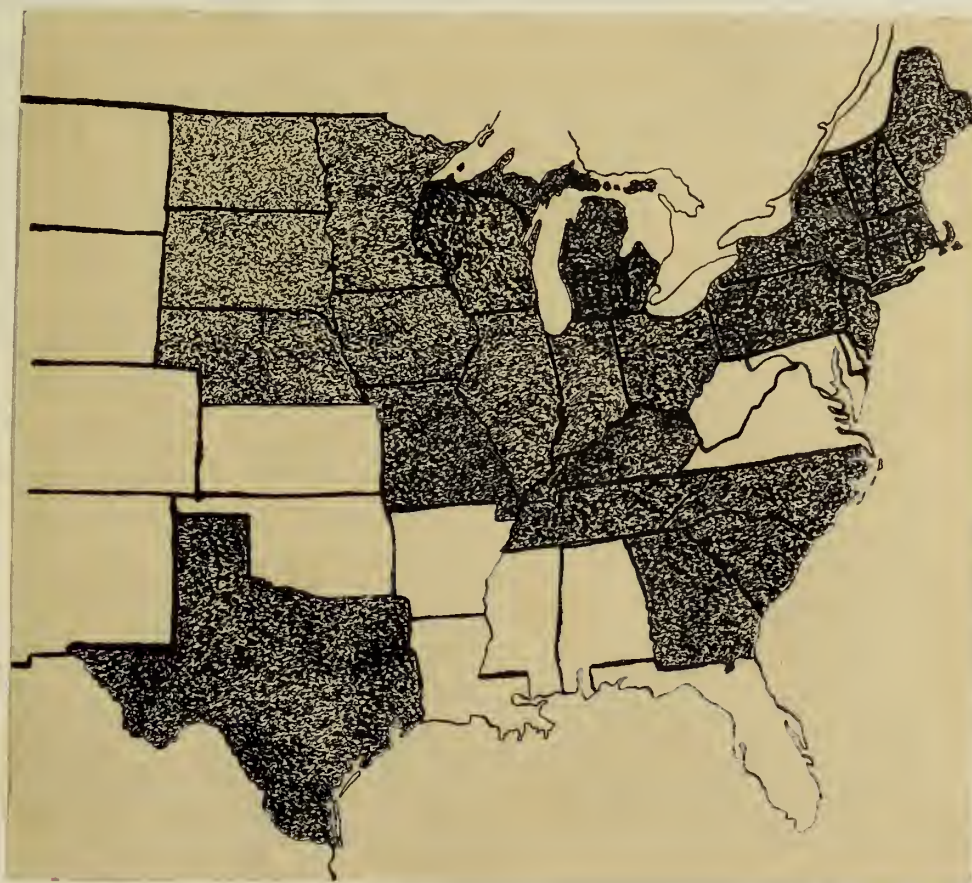
Among the fungous enemies of the elm are a number of forms which cause leaf spots, the most important of which will be discussed in this paper. Ordinarily none of these diseases is of much importance economically, but in severe cases they may injure the tree materially by causing premature defoliation. This, of course, saps the vigor of the tree, and if the severe attack is repeated during a number of consecutive seasons, may even cause the death of the tree, or at least may weaken it to such an extent that it is not able to withstand the adverse factors in its environment. In a nursery of young elm trees these leaf spots may do much more damage

than when they occur on older trees.

II. THE MOST IMPORTANT AMERICAN LEAF SPOT OF THE ELM.

DISTRIBUTION AND HISTORY.

Chief among the fungi causing leaf spots of the elm in this country is Gnomonia ulmea (Schw.) Thüm. This disease, known as the elm leaf-spot or elm leaf-scab, occurs most commonly on Ulmus americana, and is found in greater or less degree throughout the entire range of its host. The author has examined exsiccated specimens of it which were collected in the following states: New York, Massachusetts, Vermont, Maine, Pennsylvania, Michigan, Ohio, Indiana, Illinois, Wisconsin, North Dakota, South Dakota, Iowa, Nebraska, Missouri, Kentucky, Tennessee, North Carolina, South Carolina, Georgia, and Texas, as well as several from Canada. The map* (Text Figure 1) will perhaps give a



*Text Figure 1. Distribution of *Gnomonia ulmea* in the United States.

better idea of this wide distribution than does this list of states. It is more than probable that it occurs also in the remainder of the states east of the Rocky Mountains and has merely not been reported. In addition to the normal host, Ulmus americana, specimens have been examined on Ulmus fulva, U. alata, U. crassifolia, and U. racemosa, and it is quite probable that it may occur also on U. serotina, the only other American species. It has not, however, been seen on any European or other foreign elm, collected either in this country or abroad, nor is there any account in literature of its occurrence on such. It may be concluded, therefore, that this fungus is strictly an American species.

The fungus was first described by Schweinitz (34) as Xyloma ulmeum, in 1818, on leaves collected at Aiken, South Carolina. His material was immature and his description as a consequence was incomplete and inadequate. Figure 7 is a photograph of a leaf from the type collection from which his description was derived. This specimen is located, along with the remainder of Schweinitz's exsiccata in the Museum of the Academy of Natural Sciences at Philadelphia. Comparison of the above figure with Figs. 3, 4, and 5, which are photographs of infected leaves collected by the author, will serve to convince the reader that the fungus with which Schweinitz worked and the one with which the author will concern himself in the early part of this paper are identical.

A few years after Schweinitz' original description, Fries (19) in 1823 described a disease of the American elm as caused by

Sphaeria ulmea Fr., but gave Xyloma ulmeum Schw. as a synonym, showing that he had seen Schweinitz' previous description and recognized that he was dealing with the same organism. His description added but little to the earlier one of Schweinitz. The next change in the taxonomic position of the fungus was made in 1878 by Von Thümen (39) when he placed it in the genus Gnomonia without explanatory comment or additional description. Saccardo in his "Sylloge Fungorum" seems to have accepted this change with some reservations since he placed the fungus in the section Dubiae of the Sphaeriales, under the name Gnomonia ulmea (Schw.) Thüm. without, however, explaining his reasons for doing so.

In 1892 Ellis and Everhart (16) made a further change in the name and taxonomic position of the fungus, apparently without being acquainted with the prior work of Von Thümen, since they made no mention either of his name or of the genus Gnomonia in their account of the synonymy of the organism. They called it Dothidella ulmea (Schw.) E. & E., thereby placing it among the Dothidiales, though they acknowledge that it "is anomalous on account of its ascigerous cells assuming the characters of perithecia." In 1915 Thiessen and Sydow (38) in a monograph of the Dothidiales excluded it from that group and referred it back again to the genus Gnomonia in the Sphaeriales where it had previously been placed by Von Thümen. In addition to these various names, the fungus has been very much confused by American plant pathologists and mycologists with an organism causing a leaf spot of European elms in Europe, Systemma Ulmi (Schleich.) Thiess. & Syd., (38) to which it has a superficial resemblance, and it has often been collected and reported under one or another

of a various list of synonyms pertaining to that fungus.

In 1901 and 1902 Stone and Smith (37) from Massachusetts reported attempts at controlling the disease by spraying with Bordeaux mixture, referring to the fungus as Dothidea Ulmi (Duv.) Wint., a synonym of Systremma Ulmi, in the first paper, and as Dothidella ulmea, a synonym of Gnomonia ulmea, in the second, although they made no reference to the discrepancy. In 1910 Güssow (21) reported it from Canada as extending back upon the petioles of young shoots to their tips, which twisted downward and finally died. He states that in no case did the young shoots so infected recover. In this same year Clinton (8) from Connecticut reported that by July or earlier some trees had shed about all their leaves. He stated that these trees later put forth a new crop of foliage which was entirely free from the disease, but that the other trees, not so severely infected in the beginning, showed all their leaves more or less affected, and shed them continuously throughout the season. He stated that when defoliation was most severe, the young branches of the season also had fallen off. This latter observation confirms that made by Güssow in Canada. The author has not seen so severe an infection as either of these, although in some localities the disease is severe enough each year to cause an incessant dropping of leaves throughout the summer and fall, which is a far from desirable characteristic in a lawn and avenue tree like Ulmus americana.

SYMPTOMS.

The disease makes its appearance early in the spring, the amount of primary infection apparently being dependent to a considerable degree on the weather conditions, as it is much worse on the

same tree in some years than it is in others. Clinton in the report mentioned above expressed the opinion that the only infection which occurred was the primary spring infection, and that there was no further spread during the summer. The fact that no conidial or summer stage had ever been found connected with the disease, and also his observation of trees which shed all their leaves early in the season and which later produced a new crop of foliage entirely free from spots, would tend to support this conclusion. However, the absence of the disease on the new crop of leaves might have been due to weather conditions which were not favorable to the spread of the organism at that time. In any case, the author has found a conidial stage constantly associated with the disease in every specimen examined, and the connection between the two stages will be clearly shown later in the course of this paper.

The first evidence of the disease is a small whitish or yellowish fleck on the upper side of the leaf shortly after it has unfolded. The spot increases in size and soon a number of small black specks begin to appear within the whitened tissue. As these enlarge they sometimes coalesce to form a single coal-black, stroma-like, subcuticular structure which is quite irregular in outline and varies from one-half to two or three millimeters in diameter. As a rule, however, the individual stromata remain separate, when they appear to be arranged somewhat concentrically, forming a distinct spot, in most cases surrounded by a narrow band of whitish, dead tissue as shown in Fig. 12. Occasionally the black stroma, or the group of separate stromata, so closely grouped together as to seem to the naked eye to be a single one, may cover the entire dis-

colored area, without a border of whitish or lighter-colored dead tissue. In this case it appears almost like a tar-spot on the normal, green, leaf tissue and reminds one very much of some of the Rhytismas. Later in the season the cuticle which covers the stroma wears away and gives the spot an ashen appearance, which is most pronounced near the edge. These black spots may be so numerous as to practically cover the entire upper surface of the leaf.

DEVELOPMENT OF THE STROMATA.

Beneath each one of the small, black, subcuticular stromata, as represented in Fig. 13, early in its development, beginning about the latter part of May, there commences the development of the young perithecium of the causative fungus. The stroma now becomes somewhat looser in structure near its central region, beneath which the perithecium is to be formed. The normal cells of which the stromatic hyphae are made up are short, approximately isodiametrical, (Fig. 16) and contain comparatively little protoplasm, which little soon disappears, except in the basal layer of cells, and in those which are actively engaged in extending the edges of the stroma. They are more or less olivaceous to dilute brown in color, the depth of the hue depending on the age of the cell, but the very dark appearance of the stroma is due principally to a dark coloring matter which is not present in the cell wall to any extent, but seems to be excreted by the cells of the fungus and deposited between their walls. A similar excretion of coloring matter was noted by Klebahn (22) in working with Gnomonia veneta (Sacc. & Speg.) Kleb. Within the looser portion of the stroma are to be found in this stage of its development other hyphae, which are very thin walled, entirely

filled with a very dense protoplasm, and have comparatively few septa. They stain pink or red with Planeze IIIb stain (41), as do the other hyphae which enter into the formation of the young perithecium, but to a much more intense degree. The ordinary stromatic elements, which have become comparatively inactive, take a green color with this stain. These deeply staining, active hyphae ramify through the lower, looser portion of the stroma, a number of them turn upward near the center and break through to the outside, extending above the leaf surface as shown in Fig. 16.

THE ASCOGONIUM.

Immediately beneath this portion of the stroma there grows downward into the leaf tissue, between the epidermal cells and between the upper tier of palisade cells, usually to a point near the lower edge of that layer, one of these hyphae which has become slightly larger in diameter. For convenience of reference this hypha might be termed an "infection thread" or "suspensor", since it is the first of the fungal hyphae to invade the tissue of the host beneath the epidermal layer, and since in the early stages of its development the young perithecium gives the appearance of being suspended from the subcuticular stroma above by means of it. This hypha is accompanied in its growth downward into the host tissue by a number of other hyphae, consisting of short, isodiametrical cells, which arise from the basal layers of the stroma and contain comparatively little protoplasm. They form a sheath for the broader, more deeply staining hypha which for convenience of reference only has been designated as an "infection thread" or "suspensor". This, after growing to a point about midway down in the palisade layer,

cuts off a number of cells at its extreme end, (Fig. 16) usually three or four, which coil somewhat in the form of a spiral. Each one of these cells contains two or more nuclei, while the cells of the hyphae which constitute the sheath are uninucleate. These hyphae, meanwhile, have continued their growth, dividing in such a manner as to produce a larger number of chains of cells which arrange themselves spirally about the central coil and form what is to become the wall of the perithecium.

This coiled structure is the ascogonium or "Woronin's hypha" described by various authors in a considerable number of Ascomycetes. However, the hypha connecting it with the stroma above, I do not consider in any way analogous to a trichogyne, but rather as being similar to and corresponding to the hypha described by Miss Dawson (14) as leading from the stroma beneath and giving rise to "Woronin's hypha" in Poronia punctata. The apparent differences between the two cases are that in Poronia the perithecium is formed in the upper part of the stroma and the hypha which gives rise to the ascogonial coil comes up from below and does not leave the stroma, while in Gnomonia ulmea the perithecium is formed beneath the stroma in the tissue of the host, which renders it necessary for the thread which is to give rise to the ascogonium to leave the stroma and grow downward into the leaf tissue. In each case the hypha under consideration enters the perithecial primordium at a point which is finally located in the basal portion of the mature perithecium. In Poronia, however, after coiling to form the ascogonium, it continues to grow on beyond the perithecium to the outer surface of the stroma as a somewhat narrower thread, which

reminds one very much of the trichogyne of *Collema*, as described by Bachman, (3) *Physcia* by Darbishire (11), and *Polystigma* by Frank (18) and Fisch (17) but not by Blackman and Wellsford (4). This "trichogyne" was not present in *Gnomonia ulmea*.

Brooks (6) in working with *Gnomonia erythrostroma* (Auers.) Kleb. found an ascogonium similar to the one described above for *Gnomonia ulmea* and also certain structures which he designated as trichogynes. He was able to trace a connection between these hyphae and the peripheral layers of the young perithecium only, never with the ascogonium itself. These peripheral layers would correspond in Fig. 16 to the sheathing hyphae designated by a. Since more than one "trichogyne" passes through a single stoma in the case in which he is working, Brooks concludes that more than one series of "trichogynes" is connected with a single ascogonial coil. In *Gnomonia ulmea*, also, one finds (Fig. 16) as previously stated, certain hyphae which pass out through the upper leaf surface in a quite similar manner, though not through a stoma in this case, since stomata are very few on the upper surface of an elm leaf. However, in this case there is no possibility of their being mistaken for anything else than vegetative hyphae. It is quite likely that those of *Gnomonia erythrostroma* are of a similar nature. Blackman and Wellsford describe in *Polystigma rubrum* "trichogynes" similar to those of Brooks, but on account of an inability to trace a direct connection with the ascogonium, conclude that they are merely vegetative in their nature. In earlier papers Fisch (17) and Frank (18) had both described and figured such connections and had designated the hyphae

as true trichogynes.

Although Brooks continued to call the projecting hyphae in Gnomonia erythrostroma by the name of trichogynes, and, although he found both ascogonia and spermatia present, he arrived at the conclusion that the "trichogynes" were no longer functional, and that fertilization did not actually occur through their agency. He suggested as a present function for them that they might serve as respiratory channels for the fungal hyphae within the leaf, where the assimilatory processes must necessarily have been considerably curtailed by the dying of the tissue. Such a function would also give reason for the existence of similar hyphae in Gnomonia ulmea, especially since the presence of the black stroma would tend even more to impair the respiratory processes in the host tissue beneath it.

The ascogonium in the young perithecium of Gnomonia ulmea begins soon to break up into segments, each cell becoming separated from the others. H. B. Brown (7) noticed just such a segmentation of the ascogonium of Xylaria tentaculata, as did also Miss Dawson in Poronia. They found that those segments gave rise to the ascogenous hyphae in the fungi with which they were working, but I have been unable to ascertain this fact with certainty in Gnomonia ulmea with the material at hand. However, it is almost a certainty that this is the case here also since the segments of the ascogonial coil can be distinguished near the base of the perithecium until after the asci have commenced their development.

FURTHER DEVELOPMENT OF THE PERITHECIUM.

In the further development of the young perithecium all

sign of the connection with the subcutaneous stroma soon disappears, as is shown in Fig. 2, which is a photomicrograph of a slightly older stage. The structure has increased in size, chiefly by the enlargement of the portion which is later to become the perithecial cavity, but which is now filled with a dense pseudoparenchyma. The wall has also increased somewhat in thickness by the formation of new layers on the inside. As yet there is no sign of a beak or ostiole, though the wall cells on the lower side of the perithecium, opposite the stroma, are somewhat denser in protoplasmic contents, as is shown in the figure by the slightly darker color.

Fig. 8 shows a still later stage of development in which the perithecium has practically doubled in size, since the two photomicrographs are of the same degree of enlargement. The central area has enlarged and the wall has become still thicker. The darkly stained portion is composed of young asci which are not yet clearly differentiated. On account of the nature of the material, the leaves showing this stage of development having first been collected and dried and later softened with lactophenol, as well as on account of the very small size of the nuclei, the cytological and other minute details of this development could not be accurately determined. The main portion of the perithecial cavity is entirely filled with a very fine pseudoparenchymatous material, which when crushed or teased out appears merely granular in structure with some slight evidence of anastomosing hyphae. In the original description of the fungus Schweinitz mentions the granular nature of the perithecial contents. The beak or rostrum and the ostiole are here seen in the earliest stages of their development. The same group of more deeply staining

wall-cells, which are mentioned above in connection with Fig. 2, is still evident, but has increased in size so as to form a sort of plug of tissue which by its growth forces the outer layers of the perithecial wall outward and downward on the lower side to form the outer wall of the beak. As the multiplication of these actively dividing cells continues their long axis changes from horizontal, as at first, to a direction parallel to that in which the beak is being developed. The cells nearest the center of this elongating beak separate in their continued growth, leaving a channel throughout its entire length which becomes the ostiole. This channel is lined with periphyses or hair-like structures which are hyphal outgrowths of the inner or lining layer of cells. These periphyses all point in a direction outward from the perithecial cavity and so form a one-way passage from the spore-bearing portion to the outside of the leaf. As the development of the beak nears completion each layer of cells, whose increase has brought about its elongation, at its lower end produces one or more of these periphyses to each cell so that the lower end or outer opening of the ostiole is surrounded by a considerable brush of them. These later stages of the development of the ostiole are all shown in Fig. 1 which pictures two perithecia in an almost mature condition. The beaks in this figure are slightly longer than normal at this stage of maturity but in all other respects the perithecia are typical. No further elongation of the beaks occurs until the ascospores are fully mature and ready to be discharged, sometime in the early spring, at which time they again begin growth and continue until they have just broken through the lower epidermis. In the stage shown in the figure, which is the condition in which they

pass the winter, the lower end of the beak is still within the leaf tissue and merely pushes out the lower epidermis in the form of a hump or tubercle. In the spring, when they have just broken through, these beaks, though short, are quite conspicuous on account of their fresh, dark-brown or almost black color.

The asci in the figure last referred to are not yet mature and it will be seen that the pseudoparenchyma is still present. This tissue is composed of small, hyaline cells, filled with a very dense, granular protoplasm, and with very thin walls; in fact, the walls are little more than membranes. It occupies the entire central region before the development of the asci, which grow out into it, and apparently it is used up by the asci in their growth, as no crowding of the tissue is apparent ahead of them. Such an interascicular pseudoparenchyma has been described by Stevens (35) who uses it as the basis for the formation of a new genus, *Desmotascus*. In that case he considers it as an instance of delayed dissolution of the pseudoparenchymatous central region of the developing perithecium to form the central cavity. He suggests that, since this structure was not clearly seen without good, thin, microtome sections, the same thing may exist in other perithecia and have been overlooked because the microtome was not used. The finding of such a structure in Gnomonia ulmea would tend to support such an hypothesis. Reddick (29) in working with Guignardia bidwellii found that, when the first asci were developing, not nearly all the pseudoparenchyma was gone, and that, when crowded together by the growth and expansion of two asci, it gave the impression that paraphyses were present. He, also, expressed the opinion that these cells were absorbed

by the growing asci. This case differs from that found in Gnomonia ulmea and also from that described by Stevens in Desmotascus only in that the pseudoparenchymatous cells in the latter two fungi never appear to be crowded by the invasion of the asci.

The asci originate from the basal portion of the perithecial cavity and also from the sides to a point about half way to the top. The perithecial walls are seen in Fig. 1 to be composed of from ten to twelve rows of cells, the outer one or two layers of which have assumed a bright, golden-brown color. It is at about the time when the ostiole is being developed that this coloration of the wall begins. Until that time the wall has been entirely hyaline. From this time on, as the perithecia age, this color becomes constantly darker until about midwinter when it is almost black. The outer surface of the perithecium is smooth and there are no loose hyphae connecting it with the leaf tissue in which it is borne.

When mature the perithecia are nearly spherical or usually somewhat wider than deep. They vary considerably in size, but average about 250-300u in diameter and 150-200u in depth. The ostiole is usually about 100u long and 75u wide but may reach a considerably greater length. The size of the perithecium is so great that the upper epidermis is elevated in the form of small tubercles and the beaks push out the lower epidermis in the same manner, before they break through it. They do not extend any distance beyond the outer surface of the lower epidermis, as do so many of the Gnomonias, but merely reach through it. When the over-wintered leaves have been soaked in water, the perithecia may be picked out with the point of a sharp scalpel, and on account of the absence of any hyphae connect-

ing them with the leaf tissue, they leave a smooth cavity or locule in the leaf.

THE ASCI AND ASCOSPORES.

In mature perithecia one finds the asci very much confused in their arrangement. This confusion is due to the fact that the older ones are broken loose from their attachment and are pushed toward the top of the perithecial cavity by the younger ones. There are no paraphyses. The asci are oblong-cylindrical or somewhat club-shaped in form, and have a short stalk at the base which may be either straight or bent toward one side. The wall is hyaline, thin below, but thickened in the upper half, (Fig. 19) and does not color with iodine. At the upper end of the ascus is a pore surrounded by a ring of thickened tissue which is strongly refractive toward light. In optical section as seen from the side this ring presents the appearance of two small spheres arranged side by side in the apex of the ascus. The asci measure 45-55 x 9-11 μ .

The spores are very characteristic also. They are hyaline, elongate-elliptical, or obovate-oblong, and have a septum near the lower end, thus becoming unequally two-celled. They are eight in number, sub-biseriate, and measure 8-10 x 3-3 $\frac{1}{2}$ μ . The small cell at the lower end of the spore averages about 2 μ both in length and breadth. There is a slight constriction at the septum. Some epiplasm is present in the mature ascus along with the spores.

EXPULSION AND GERMINATION OF ASCOSPORES.

As mentioned above, the asci in a mature perithecium become loosened from their attachment at the base and crowded toward the apex of the perithecial cavity in a somewhat disordered mass.

In the process of expulsion of ascospores an entire ascus enters the lower part of the ostiole and is held in place by the periphyses until the pressure produced by the absorption of water, which must be present to allow of ascospore discharge, becomes sufficient to bring about the discharge of the spores. These pass outward through the periphyses-lined ostiolar channel to the surface of the ostiole where they are expelled with some force and under natural conditions are evidently dispersed by currents of air. Early in March leaves were found, which had passed the winter in the open under natural conditions, on which occurred perithecia in such a stage of development as to expel ascospores within two days after being brought into the laboratory. It was found that spore expulsion was very slow and limited or did not occur at all when the leaves were kept too moist or when maintained in a saturated atmosphere, such as occurs when they are placed on moistened filter or blotting paper in a closed Petri dish. However, when the lid of the dish is removed and the leaves are alternately allowed to become dry and again moistened by adding water to the filter paper beneath them, the spores are expelled in considerable quantities. If they are then caught on a glass slide, either dry or coated with a thin film of egg albumin, glycerine or some such adhesive, it is found that the spores are deposited in clusters or groups of eight. Later, as a very large number of spores are discharged from a single ostiole, this grouping is, of course, not apparent. The best means found for catching the expelled spores was that used by Anderson and Rankin (1) in working with Endothia parasitica, as described above. The glass slide was suspended by means of match sticks fastened to it

near the ends thus bringing it three or four millimeters above the opening of the ostiole.

Klebahn (27) has shown that the method of spore expulsion described above is general to the *Gnomonias* and to many other fungi which have *Gnomonia*-like, beaked ostioles. The expulsion of the asci into the neck of the ostiole appears largely due to the swelling pressure of the ascus. When dry, the ascus with its contained spores occupies considerably smaller space than after it has been moistened with water. Many authors have maintained that ascospores are ordinarily liberated one at a time, and such may be the case here, since I have been unable to observe the actual act of expulsion of the spores from the ascus, but the clusters of the spores intercepted on a glass slide suspended above the opening of the ostiole are always in groups of eight, and give the impression of having been expelled in a group as was found by Anderson and Rankin to occur in *Endothia parasitica*.

Many attempts have been made to germinate the ascospores of *Gnomonia ulmea* under many and various conditions, and on a number of different nutrient media, ranging from distilled water, tap-water, extract of dried elm leaves, and sugar solutions to solid media such as corn-meal, bean, potato, Brazil nut, onion, elm-leaf, and plain washed agar. In distilled or tap water the spores swelled considerably, especially the larger cell, and sometimes a spore would give the appearance of being on the point of sending out a germ tube from the side of the larger cell but this never occurred. This is in accordance with the results obtained by Klebahn (27) in *Gnomonia alniella* and *Gnomoniella tubiformis*, which he was not able

to grow in culture, but is contrary to his results with Gnomonia platani and Gnomonia leptostyla, both of which grew well on nutrient media, the latter even going so far as to produce the perithecial stage in such cultures. It would seem that the ascospores of Gnomonia ulmea, as in Gnomonia alniella and Gnomoniella tubiformis, require the stimulation given by the green leaf of the host plant itself in order to induce germination. Wolf (42) found that this was the case in Diplocarpon rosae, the ascospores of which would not even germinate in a drop of water in which a portion of a green leaf of the host had been placed, but must be placed in a drop of water directly on the living leaf itself.

OBSERVATIONS ON OVERWINTERING OF THE FUNGUS.

A number of observations have been made on the overwintering of the fungus on elm leaves under various conditions, and some attempts have been made to hasten its development by placing the leaves under various controlled conditions. Leaves on which the spots occurred were brought into the laboratory, both before and after they had been severely frosted, and some were immersed in water, both at room temperature and in the refrigerator, others were placed in a moist chamber suspended over water both in the laboratory and refrigerator, and others were placed in each of these places under their normal conditions of humidity. Still others were suspended over calcium chloride in each of these temperatures in order to assure a dry atmosphere. It was found that no further development occurred in the leaves which were immersed in water and that the fungus soon died, the perithecia becoming mere empty husks. This observation was confirmed by comparison with leaves which had

wintered normally outside the laboratory. On leaves which had been buried slightly in the soil or were in close contact with the soil underneath a layer of other leaves, the perithecia were found in early spring to be in approximately the same condition. No further development of the fungus occurred on the leaves either suspended above the calcium chloride or in the normal humidity conditions of the laboratory or of the refrigerator. However, the fungus in the leaves which had been suspended above water in a moist chamber did continue their development and by midwinter a few perithecia were found in which the spores were apparently practically mature. In most, and finally in all cases, however, numerous saprophytes developed in such abundance that the *Gnomonia* fungus was overgrown and destroyed before the spores could mature. Other leaves from outdoors were brought into the laboratory at various times throughout the winter and placed in moist chambers, but the same development of extraneous saprophytes soon stopped the observations. In a number of instances observed, the *Gnomonia*, apparently in an effort to counteract and overcome the encroachments of the more rapidly developing saprophytic fungi, began to grow vegetatively and the entire perithecial cavity as well as the ostiolar canal became filled with a mass of interlaced and anastomosed hyphae, so compacted together that under pressure the perithecial wall would break away but the interior mass would tend to retain its spherical shape. However, this tissue later died and disintegrated, leaving the empty husk of the perithecium. Among the saprophytes which hindered observations a number of forms were invariably present. They were in the main, *Cephalothecium roseum*,

Phycomyces nitens, several species of *Penicillium* and *Aspergillus*, an *Alternaria*, a *Pleospora*, a *Cryptostyctis*, and a *Myxomycete*.

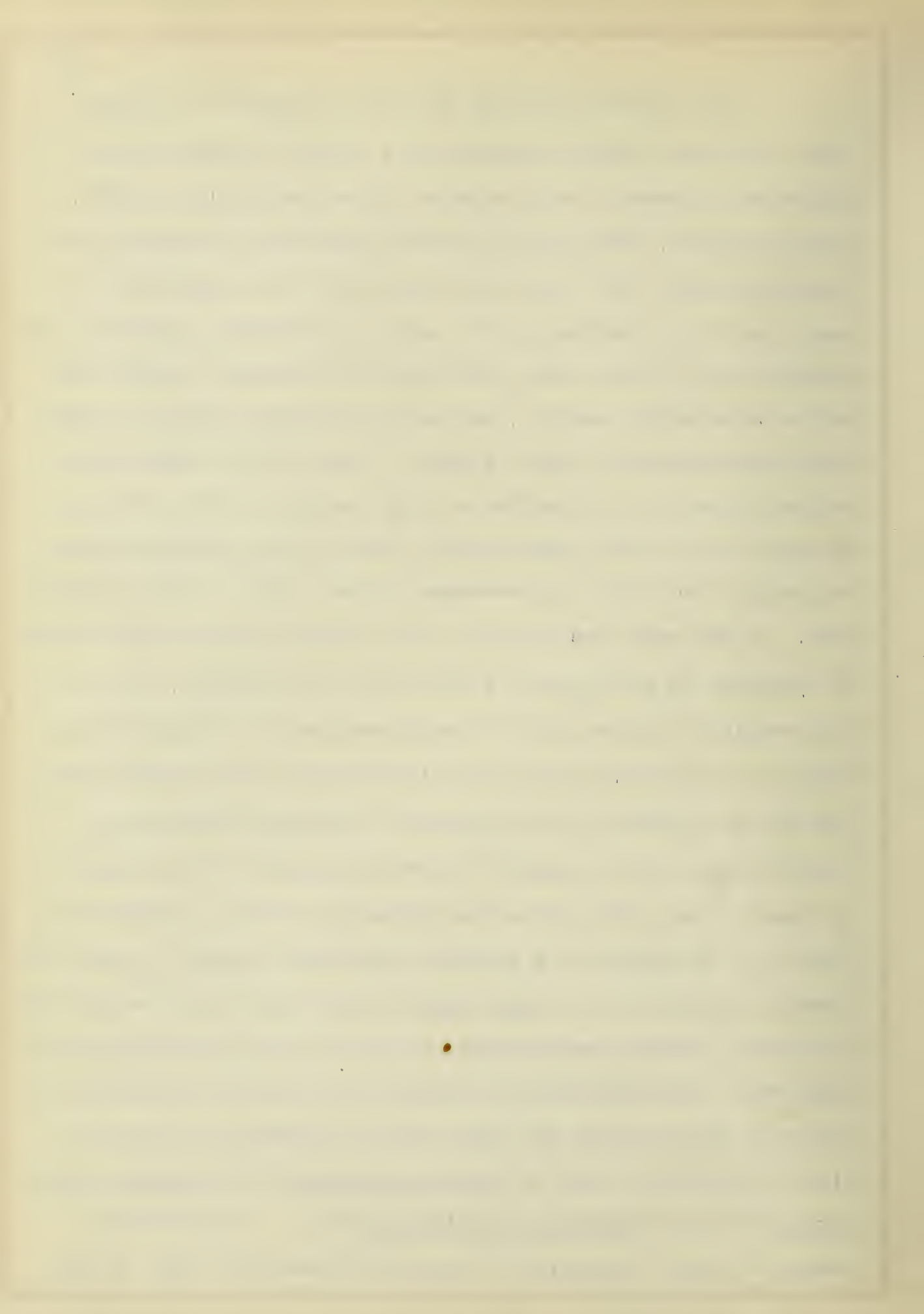
Various observations also were made on leaves wintered outside the laboratory. Some leaves were placed on shelves of a wire cage, others were placed on the ground and covered with other leaves and soil, while still others were wrapped in cheese cloth and placed on the surface of the ground. In the leaves placed on the shelves and on the surface of the ground, the fungus was found to mature more rapidly than on those leaves covered with other leaves and soil, and a very few perithecia were found on such, which contained some spores apparently almost mature as early as the middle of February. On only one leaf, however, were any of the perithecia at that time mature enough to expel spores. This leaf was on the shelf of the wire cage, which was placed directly against the south wall of the greenhouse, and was exposed both to the direct rays of the sun and also to the heat rays radiated from the cement wall. In most cases at that time the asci were somewhat more developed than when observed in the fall, but the spores were not yet differentiated. The normal development during the winter, therefore, seems to be very slow. In leaves which were in especially damp situations, as those buried in the soil or those in intimate contact with the soil under a cover of other leaves, most of the perithecia were found to be dead and disintegrated. In general, it seemed that leaves neither in too exposed nor too moist a situation, as, for instance, those toward the middle of a pile of leaves, showed the greatest development of the fungus late in winter and early in the spring.

CONIDIAL STAGE.

In every specimen examined in which this ascigerous stage of Gnomonia ulmea occurred, I have found constantly associated with it an imperfect or conidial form. This stage was found present from early spring until late fall on every leaf collected, and also on all exsiccata material examined, even the Schweinitzian type specimen to which previous mention has been made. I have examined all available published exsiccata specimens of Gnomonia ulmea as well as more than a hundred other specimens obtained for purposes of comparison from various educational institutions and private individuals, including several from the Royal Botanical Gardens, Kew, England, and the herbarium of the University of Geneva, Geneva, Switzerland. The published exsiccata specimens examined are as follows: Ravenel Fun. Am. Exs. No. 752; Ravenel Fun. Carol., Fasc. II, No. 63; Ellis and Everhart Fun. Col. Nos. 239, 2928, and 3422; Seymour and Earle Econ. Fun. Nos. 155a and 155b; Ellis N. Am. Fun. No. 1347; Brenckle Fun. Dakotensis No. 329; Rabenhorst-Winter Fun. Eur. Nos. 3661a and 3661b; and DeThümen Myc. Univ. No. 1155.

The conidial layer develops on the stroma which is found on the upper surface of the leaf above the base of the young perithecium (Fig. 14). It may cover only a portion of the stroma and there may be two or even more of them on a single one of the stromata. Again, a stroma may develop, to all appearances identical with those formed above the bases of the young perithecia, but the perithecium be lacking. In this case the conidial pustule invariably covers the entire surface of the stroma.

The conidial pustules are quite irregular in outline, (Fig. 18) though usually approaching a somewhat circular shape, unless two or more of them coalesce, which frequently, in fact, usually, happens, when they may become considerably elongated and variously lobed. The size also varies to a very considerable extent, due to the coalescing of a number of different pustules. The average size is about half a millimeter in diameter, though they may be considerably smaller, and have been seen as large as eight-tenths millimeter. The upper layers of cells of the subcuticular stroma elongate in a direction at right angles to the surface of the leaf and form the conidiophores. These press closely against the cuticle and lift it up somewhat in the course of their development. At the same time they give off a brown coloring matter which is deposited on the inner or lower side of the cuticle, which itself remains colorless. This coloring substance is deposited more deeply at the points between the conidiophores than directly above them so the darkened cuticle presents a somewhat reticulate or netted marking, and on casual observation appears to be composed of fungal tissue. This gives the impression that the conidial pustule is of the nature of a dimidiate pycnidium. However, closer observation shows that no fungal hyphae enter into this covering layer and the structure consequently is found to be melanconiaceus in character. The deposition of coloring matter on the cuticular coverings of such acervuli has been noted by Klebahn in connection with the conidial stages of Gnomonia padicola (23), Gnomonia leptostroma (22), and Gnomoniella tubiformis (21). As previously stated, the same substance is deposited between the cells of the



hyphae which make up the stroma, and which now have become the cells of the hymenial layer from which the conidiophores arise. It is also frequently found deposited between the cells of the epidermis immediately beneath the stroma.

These epidermal cells are not changed to any considerable extent except for crystalline substances which one occasionally finds deposited in them. The fungal hyphae grow down between them and crowd them apart somewhat, but they do not lose their arrangement as a definite layer. The hyphae of the fungus do not penetrate the cells of the host. The conidiophores are crowded together into a very compact layer and are 8-12u in length by 1.5-2.5u thick. They are without septa, except for an occasional one near the base, and terminate in a thread-like projection on which the spores are borne. The conidia are elongate-oblong, or cylindric, bacillar, pointed at one or both ends, straight or sometimes slightly curved, one-celled, hyaline, and measure 5-6 x 1-1.5u. (Fig. 15).

Since there is no fungal covering to the conidial layer the fungus falls into the family Melanconiaceae, and its other characters indicate beyond a doubt that it is a member of the genus Gloeosporium. It seems to be quite characteristic of the Gnomonias to have a conidial stage which is melanconiaceous in character. Gnomonia padicola has as an imperfect stage Asteroma Padi, but according to Klebahn (20) no true pycnidium is formed. Gloeosporium nervisequum is connected with Gnomonia veneta, Marssonina Juglandis with Gnomonia leptostyla, Gloeosporium quercinum with Gnomonia quercina, Gloeosporium Caryae with Gnomonia Caryae, Gloeosporium Tiliae with Gnomonia Tiliae, and Leptothyrium alneum with Gnomoniella tubiformis. Klebahn(21)

has shown also in connection with Leptothyrium alneum that no true pycnidial covering is formed and it is consequently melanconiaceous in structure. Saccardo (26) also remarks concerning this species "(perithecio) subinde tamen spurio et ex epidermide mutata et atrata formato."

The genus Gnomonia contains a number of species which form no conidial stage, or, at least, whose conidial stage has not yet been discovered. In so far, however, as the conidial stages have been established in the genus, it is clearly evident from the above that they conform to a more or less close resemblance to the genus Gloeosporium. The Leptothyrium of Gnomoniella tubiformis is scarcely to be distinguished from a Gloeosporium; Asteroma of Gnomonia padicola differs from it only in the production of superficial mycelium, and Marssonina of Gnomonia leptostyla only in its two-celled conidia.

Among the many fungous diseases occurring on the leaves of the elm only a few have been found whose causative organisms are located in the family Melanconiaceae. Three of these belong to the American flora, namely, Coryneum tumoricolum Peck, Septogloeum profusum (Ell. and Ev.) Sacc., and Cylindrosporium ulmicolum Ell. and Ev. I have not seen Ellis and Everhart's specimen of Cylindrosporium ulmicolum and it may be identical with Phleospora Ulmi (Fr.) Wallr. since the two descriptions appear very much alike. Septogloeum profusum has been reported as occurring on the leaves of Ulmus alata and Ulmus americana though it was originally described on Corylus americana. Two species of Gloeosporium, or rather one species and a variety of the same, have been described on the elm in Europe. One of these, Gloeosporium inconspicuum Cav. was described on Ulmus

americana in Italy but has never been reported in this country. It was distributed by Briosi and Cavara in "Funghi parassiti" as No. 350. It causes large, ochraceous spots on the upper side of the leaf, and has very small, bacteriform spores, only 1-2u in length. A variety of this species, Gloeosporium inconspicuum Cav. var. campestris Dor. (15) has been described on Ulmus campestris in Russia. This, from the description, is quite similar in external appearance to the above species, but the spores and conidiophores are considerably larger, the spores measuring 3-6 (sometimes 9) x 1-2u. The fungus described above as occurring on Ulmus americana and other species of elm in America in connection with Gnomonia ulmea does not agree in any particular with any of these, and I, therefore, advance for it the name of Gloeosporium ulmeum. A formal description is given immediately following.

GLOEOSPORIUM ULMEUM SP. NOV.

Acervuli somewhat gregarious, often confluent, borne on black stromata, usually over the base of the developing perithecium of Gnomonia ulmea, covered by the darkened cuticle, which later splits and cracks irregularly and finally breaks away entirely, subrotund or irregular, averaging 500u in diameter, but often as large as 800u, epiphyllous, very rarely hypophyllous; conidiophores cylindrical, crowded, occasionally with a septum near the base, 8-12 x 1.5-2u, terminating in a thread-like projection on which the spores are borne; conidia elongate-oblong or cylindric, bacillar, pointed at one or both ends, straight or very slightly curved, hyaline, one-celled, 5-6 x 1-1.5u.

Habitat, on living leaves of Ulmus americana, U. fulva,

U. alata, U. racemosa, and U. crassifolia. Common. ____ Conidial stage of Gnomonia ulmea (Schw.) Thüm. and constantly associated with it. Type specimen on Ulmus americana, collected at Urbana, Illinois, August, 1919, and deposited in the Herbarium of the University of Illinois. ____ Differs from Gloeosporium inconspicuum Cav. in the very different appearance of the spots, and in its larger spores, and from Gloeosporium inconspicuum Cav. var. campestris Dor. in the character of the spots.

III ANOTHER GLOEOSPORIUM ON ELM.

While working with the above fungus I encountered a single tree in a nursery at Oconomowoc, Wisconsin, on which the leaf-spots were quite different in external appearance from those on the surrounding trees, most of which were abundantly spotted with the Gnomonia disease, although the trees were of the same species and had apparently been planted at the same time. Figure 9 shows a photograph from this collection.

The leaf-spot is raised considerably more than is the case in the above described species, giving the portion of the leaf on which it occurs a crumpled appearance where the spot becomes large, and is confined quite closely to the leaf veins, along which it spreads, often extending the entire distance from the midrib to the edge of the leaf, thus forming elongated streaks. The leaf veins also become browned for quite a distance beyond the spots, though the remainder of the leaf is a normal green. The spots present a gray salt-and-pepper aspect, due to the whitened epidermis over which the black conidial pustules are thickly scattered. The whiten-

ed appearance is due also to the disappearance of the contents of the epidermal cells and of the cells of the palisade layer immediately beneath them. This disappearance of cell contents is much more pronounced than in the Gnomonia ulmea spot.

The acervuli are very numerous in a single spot and are quite commonly confluent. They are orbicular to oblong in shape, very irregular in outline, and are covered by the darkened cuticle which persists for a long time, finally cracking and breaking irregularly to allow the dispersal of the spores. They average 800u in diameter. The hymenial layer is pseudoparenchymatous, composed of practically colorless cells which are almost isodiametrical in shape. This layer may be even thicker than that described above in the case of Gloeosporium ulmeum, though it presents an entirely different appearance, and on account of the absence of color does not at all suggest a stromatic base. The layer appears even thicker than it really is on account of the absence of all color from the epidermal cells, which have become entirely filled with small colorless crystals. This is true to a lesser extent of the adjacent layers of palisade tissue. The conidiophores are closely packed together, and are quite similar to those of Gloeosporium ulmeum except for their larger measurements, being 10-15 x 2-3u. They are not as darkly colored as are those of the above species though they are not entirely hyaline. The apex is rather blunt and the conidiophore terminates rather abruptly in a sterigma-like projection on which the spores are borne. Occasionally two of these sterigma-like processes occur on a single conidiophore. The conidia are much larger, both

in length and width, and vary considerably in form, from oblong-cylindric to ovate, elliptical, and even pyriform. They measure 7-10 x 3-3.5u. (Fig. 17), are one-celled, rounded at both ends, straight, and are hyaline. In no case was the perithecium of *Gnomonia* or any similar fungus found associated with this spot. I consider it as being entirely distinct from the conidial stage of *Gnomonia ulmea* and propose for the fungus the name of *Gloeosporium ulmicolum*. A formal description is given below.

GLOEOSPORIUM ULMICOLUM SP. NOV.

Spots epiphyllous, raised, gray on account of the black acervuli thickly scattered over the whitened epidermal cells, elongated, following the leaf veins, often extending the entire length of the secondary veins which have become browned far beyond the limits of the spot; acervuli epiphyllous, gregarious, subcutaneous, covered by the persistent, darkened cuticle which finally ruptures irregularly to allow the dispersal of the spores, averaging 800u in diameter, irregular in outline but usually elongated suborbicular; conidiophores in a closely packed layer, dilute-brown, cylindrical, usually nonseptate but occasionally with a septum near the base, seated on a pseudoparenchymatous hymenial base which is colorless, 10-15 x 2-3u, terminating rather abruptly at the apex in a sterigma-like projection on which the spores are borne; conidia hyaline, one-celled, straight, rounded at both ends, oblong-cylindric, ovate, elliptical, or even pyriform, 7-10 x 3-3.5u.

Habitat on living leaves of *Ulmus americana*. Oconomowoc, Wisconsin, August 22, 1919. Type specimen deposited in the Herbar-

ium of the University of Illinois. This species differs from Gloeosporium ulmeum in the shape and appearance of the spots, in the fact that it is not associated with a perithecial stage as that fungus constantly is, in the absence of a black basal stroma, and in the larger spores. In external appearance the two forms are quite distinct. It differs also from Gloeosporium inconspicuum Cav., and from Gloeosporium inconspicuum Cav. var. campestris Dor. in the character and appearance of the spot and in the much larger spores.

IV.. THE PRINCIPAL EUROPEAN LEAF SPOT OF THE ELM.

SYSTEMMA ULMI (SCHLEICH.) THIESS. AND SYD.

The leaf spot of the elm occurring in Europe on Ulmus campestris, U. effusa and U. glabra, has a somewhat superficial resemblance to that produced in this country by Gnomonia ulmea (Schw.) Thüm. This may be readily seen by comparing Fig. 6 which is a photograph of the European spot on a leaf of Ulmus campestris with Figs. 4 and 5 which are photographs of leaves of Ulmus americana affected by the Gnomonia. The two diseases have been much confused in this country, and it has been quite a common thing for American plant pathologists and mycologists to speak of the latter fungus under the name of the European organism. In examining specimens of the Gnomonia spot in various collections in this country I have found it quite as often referred to in this manner as under its true name or synonyms. There are two references in literature to the occurrence of the disease caused by Systemma Ulmi in America in addition to various others which are clearly due to a confusion of the two forms. In one of these cases, the report by Trelease

(40) of the presence in Wisconsin of Phyllachora Ulmi Fuck., which name is a synonym of Systemma Ulmi, I found on examination of the specimen, which is located in the Museum of the Shaw Botanical Gardens at St. Louis, Missouri, that the disease was the American form, caused by Gnomonia ulmea. Trelease also reported the presence on the same leaf of Septoria Ulmi Fr., a synonym of Phleospora Ulmi (Fr.) Wallr., which at that time was thought to be the conidial stage of Phyllachora Ulmi, but I was unable to find any trace of it on the specimen examined. In material sent me from the University of Geneva, at Geneva, Switzerland, I found another specimen, evidently from this same collection by Trelease and labeled in the same manner. It also was Gnomonia ulmea.

The second reference to the occurrence of Systemma Ulmi in this country is made by Ellis and Everhart (16) who state that a specimen of Dothidella Ulmi (Duv.) Wint., which name is merely another of the numerous synonyms under which the European organism is known, was sent to Schweinitz by Dr. Torrey from New York state. The authors add that they do not find any other references to this species being found in this country, and that they have seen no American specimens. I find in Saccardo's (33) *Sylloge Fungorum* in the description of Sphaeria apertiuscula Schw. on Ulmus fulva, collected by Torrey in New York, the statement added that the upper side of the leaf is covered with Dothidea Ulmi. This is evidently the specimen to which Ellis and Everhart were referring, as both the names used are synonyms of Systemma Ulmi. I have not seen this specimen, and there is a possibility that it is really a specimen

of the European leaf spot, but it is hardly likely, especially since it has never been collected in this country since, nor has it ever been reported as occurring on Ulmus fulva at any other time, either previous to that collection or later.

I find in specimens sent me from the Royal Botanical Gardens, at Kew, England, among those labeled as belonging to the herbarium of Berkeley, three specimens purporting to have been collected by Drummond in Arctic America. These were undoubtedly specimens of Systremma Ulmi, and, though the host was not named, the leaves possessed the somewhat three-lobed character peculiar to the Scotch elm, Ulmus glabra. This species of elm is not native to America, and one would hardly expect to encounter an introduced species in the Arctic regions. For these various reasons I believe that the above mentioned three specimens represent some European collection which has in some manner accidentally become mixed with Drummond's Arctic collections while they were in the process of being mounted at the museum. This seems all the more probable when it is noted that the handwriting on the labels is the same as that on a great many of the other specimens from the same museum. It would seem, therefore, quite probable that Systremma Ulmi does not occur at all in America.

Although Ellis and Everhart place the causative organisms of the two diseases in the same genus they express a caution against confusing the two, stating that although they have spores essentially the same they differ very markedly in other characteristics. In spite of the fact that the external appearance of the two spots seems quite similar to the casual observer, as soon as one sections

them the very marked differences between the two fungi becomes apparent. Fig. 10 represents a photomicrograph of a section through the stroma of Systemma Ulmi. It will be seen at once that the black stroma, to which the external resemblance between the two forms is due, is in this case subepidermal, while in Gnomonia ulmea it is subcuticular only. In the Systemma the asci are produced in locules without true perithecial walls, which are imbedded in the stroma and open on the upper side of the leaf, while in Gnomonia the perithecia, truly sphaeriaceous in character, are located in the leaf tissue beneath the stroma and open on the under side of the leaf. Gnomonia ulmea, therefore, belongs to the Sphaeriales, while Systemma Ulmi belongs to an entirely different order, the Dothidiales. Although the asci and spores of the two differ but little in form, both are slightly larger in Systemma than in Gnomonia.

I have examined all available published exsiccati specimens of this fungus as well as about two hundred other specimens borrowed for purposes of examination and comparison from the Royal Botanical Gardens, at Kew, England, and from the University of Geneva, Geneva, Switzerland, and from a number of institutions and individuals in this country. The published exsiccati of this fungus examined are as follows: Berkeley Brit. Fun. No. 192; Vize Mic.-Fun. Brit.No.277; Cooke Fun. Brit., Ser. I, No. 184; Briosi and Cavara Fun. parass. No. 73; Pollacci Fun. Longobardiae Exs. No. 287; Saccardo Myc. Ven. Nos. 231, and 642; Roume~~e~~re Fun. Sel. Exs. Nos. 466, and 5761; Fl. Gall. et Germ. Exs. No. 1000; Schleicher Crypt. Exs. No. 73; Holl, Schmidt, und Kunze Deut. Schwämme No. 32; Desmazières Crypt. Fr., Ser. I, No. 284; Mongier et Nestler Stirpes Crypt. No. 766; DeThümen Fun. Austr. No. 499; DeThümen Myc. Univ. No. 2064; Fuckel

Fun. Rhen. Nos. 1013 and 2265; Sydow Myc. Mart. No. 256; Lundh. Fun. Hung. No. 374; Rabenhorst Herb. Myc. No. 658; Westend. Herb. Crypt. No. 111; Krueger Fun. Sax. No. 1514; Eriksson F. Scand. Nos. 292a and 292b.

The synonymy of the fungus is as follows:

Systemma Ulmi (Schleich.) Thiess. and Syd., Die Dothidiales, Ann. Myc. 13:334 (1915).

Sphaeria Ulmi Schleich., Crypt. exs. no. 73, sec. de Candolle Fl. Franc. II, p. 288, (1805).

Sphaeria xylomoides DC., Fl. Franc. II, p. 288 (1805).

Sphaeria Ulmi Duv., Hoppe's Bot. Taschenb., p. 105 (1809).

Xyloma sticticum Mart., Crypt. Flor Erlang., p. 309 (1817).

Sphaeria Ulmaria Sow., Eng. Fun., Tab. 374, fig. 3.

Polystigma Ulmi Link, Rab. Handb. I, p. 167.

Dothidea Ulmi Fr., Syst. II, p. 555 (1823).

Phyllachora Ulmi Fuck., Symb. p. 218; Sacc. Syll. Fun. II p. 594 (1883).

Euryachora Ulmi Schroeter, Crypt. Fl. Schles. 3 Bd. II, p. 473.

The conidial stage of this fungus is Piggotia astroidea B. and Br.

V. OTHER LEAF SPOTS OF THE ELM.

IN AMERICA.

MYCOSPHAERELLA ULMI KLEB.

Mycosphaerella Ulmi Kleb. (28) is the ascigerous stage of Phleospora Ulmi (Fr.) Wallr. which has been reported both in America and Europe as the cause of a leaf spot on Ulmus campestris,

U. glabra, and U. americana. In the conidial stage it is said to sometimes do considerable damage to nursery stock and young trees. Stewart (36) states that it has been observed several times to cause extensive defoliation of young elms in New York. Numerous small reddish-brown spots appear on the upper side of the leaves which in consequence gradually turn yellow, the margin becomes brown and rolls up, and they fall early in the season. The spores ooze out in minute cirrhi which dry on the lower side of the leaf surface and form small whitish patches. Saccardo (31) states that on account of pycnidia being absent it leans toward Septogloeum, and it is sometimes known by that name. Clinton (9) and Briosi and Cavara (5) also maintain that it belongs to that genus and call it Septogloeum Ulmi (Fr.) Bri. and Cav. Clinton also suggests that Cylindrosporium ulmicolum Ell. and Ev. is possibly not distinct from this species. I have not seen the Ellis and Everhart specimen and one must admit that the two descriptions are very similar, especially when one takes into consideration the very great differences in spore measurements recorded by various collectors of Phleospora Ulmi. Stewart records as follows: "As we have found them, they (the spores) are 3-4-septate, usually quite strongly curved, and measure 34-38 x 5.5-6.5u. In No. 157 of Seymour and Earle's Economic Fungi, on Ulmus fulva, the spores are 3-septate, straight, and measure 33.5 x 6.3u. In No. 648 of Krieger's Fungi Saxonici, on Ulmus campestris, they are 3-4-septate, strongly curved, and measure 49.5 x 4.7u." Under the name of Septoria Ulmi Fr., this fungus was attributed by Fuckel to be the spermagonial stage of Phyllachora Ulmi, a synonym of Systemma Ulmi, but it was shown by Klebahn (23) that it had no connection with that

fungus, but was the conidial stage of Mycosphaerella Ulmi, which develops on the dead leaves in the spring.

CYLINDROSPORIUM ULMICOLUM ELL. AND EV.

Spots becoming flavous; acervuli minute, hypophyllous; conidia cylindraceous, 45-65 x 4u, hyaline, multinucleate, coming out in minute white caespitules. Reported on leaves of Ulmus alata in Mississippi. In spite of the differences in spore measurements the possibility has been suggested that this is not different from Phleospora Ulmi.

SEPTOGLOEUM PROFUSUM (ELL. AND EV.) SACC.

Spots epiphyllous, flavous; acervuli scattered, hypophyllous, large; conidia coming out in white cirrhi, cylindrical, oblong, granular, 3-septate, 25-30 x 6-7u. Reported on living leaves of Ulmus americana and Ulmus alata, although it was first described on Corylus americana.

CERATOPHORUM ULMICOLUM ELL. AND HARK.

Causes small, suborbicular, dirty-brown, amphigenous spots with a white center, one-half to one centimeter in diameter, on living leaves of Ulmus fulva. Noted from several places in the United States.

PHYLLOSTICTA ULMICOLA SACC.

Reported as being present in Wisconsin by Davis (13) who remarks as follows: "Under this name I am recording the occurrence of a fungus having the following characteristics: Spots indefinite, immarginate, orbicular, light-brown, becoming cinerous above and lacerate, finally falling away in fragments, 3-7 millimeters in diameter, sometimes confluent; pycnidia epiphyllous, scattered, black, globose to depressed, 60-80u; sporules globose to elliptical, oliva-

ceous-hyaline, continuous, 3-6 x 2-3u. On Ulmus americana, Tisch Mills, August 3, 1917. Ulmus racemosa, August 5, 1917. This is probably a member of a group of forms to which various names have been applied in Europe and America." It has also been reported from a number of other states, among them being Michigan where it is said to occur on Ulmus fulva.

PHYLLOSTICTA CONFERTISSIMA ELL. AND EV.

Spots red-black, amphigenous; pycnidia 75u in diameter; spores allantoid, hyaline, 3-4 x 1u. On leaves of Ulmus fulva in Kansas.

PHOMA CINCTA B. AND C.

Spots irregular, depressed, with a white border; spores oblong, narrow, 6-8u long. Reported on leaves of Ulmus americana in South Carolina.

EXCIPULA ULMICOLA SCHW.

Causes widely expanded, indeterminate spots on the upper side of the leaf, becoming somewhat spotted with gray on both sides, with a broad, fuscous margin; pycnidia copious, immersed, excipuloid, punctiform, black, depressed in center and becoming gray. Reported as somewhat rare on cast-off leaves of Ulmus fulva about Bethlehem, Pennsylvania.

CORYNEUM TUMORICOLUM PECK.

Forming scattered, suborbicular, pale spots, bounded by a red-brown border on living leaves of Ulmus americana in the Adirondack mountains.

SPHAERIA APERTIUSCULA SCHW.

Scattered, fuscous-black, minute, arising from the swollen

parenchyma, at first innate; at length opening by a very wide mouth, but evacuate within; resembles a small *Peziza*. Recorded as occurring on the lower side of leaves of *Ulmus fulva* in New York.

RHYTISMA ULMI FR.

Minute, difformous, gyrose with an elevated margin at length dehiscing labiately. Reported on leaves of *Ulmus* in North America.

MELASMIA ULMICOLA B. AND C.

Spots reddish, indefinite; pycnidia punctiform; spores minute, oblong-botuliform. Cook (10) speaks of it as the *Melasmia* stage of *Rhytisma Ulmi* and reports it as very common in New Jersey.

A LIST OF THE OTHER LEAF SPOTS OF ELM OCCURRING IN EUROPE ONLY.

Acremoniella pallida Cooke and Mass., *Actinonema Ulmi* Alleschr., *Ascochyta ulmella* Sacc., *Asteroma angulatum* Desm., *Asteroma Fuckelii* Sacc., *Cladosporium hypophyllum* Fuck., *Exoascus campester* Sacc., *Gloeosporium inconspicuum* Cav., *Gloeosporium inconspicuum* Cav. var. *campestris* Dor., *Laestadia comedens* (Pass.) Sacc., *Pestalozzia maculicola* Rostr., *Phyllosticta bellunensis* Mart., *Phyllosticta lacerans* Pass., *Phyllosticta ulmaria* Pass., *Phyllosticta Ulmi* West., *Sphaerella Oedema* (Fr.) Fuck., *Sphaerella insularis* Wallr., *Sphaeria ulmifolia* Pass., *Sporodesmium Ulmi* Fuck., *Stagnospora ulmifolia* (Pass.) Sacc., *Stigmella Castagneana* (Mont.) Sacc., and *Taphrina Ulmi* Johans.

FOSSIL LEAF SPOTS OF THE ELM.

In Meschinelli's "Fungorum Fossilium Iconographia" I find seven species occurring on leaves of fossil elms. Plates and figures are given of six of these but they are very unsatisfactory in most cases, and in some instances one can not be at all sure that the spot

is even of fungal origin. The species are listed here: Sphaerites perforans Goepp., Sphaerites glomeratus (Engelh.) Mesch., Sphaerites rhytismoides (Ettingsh.) Mesch., Rhytismites ulmicola (Ettingsh.) Mesch., Rhytismites Ulmi (Ludw.) Mesch., Depazites Ulmi (Ettingsh.) Mesch., and Xylomites sp. (Boulay) Mesch.

VI. SUMMARY.

1. Gnomonia ulmea (Schw.) Thüm., the cause of the most common elm leaf spot in America, has been reported as occurring on five of the six native species of elm in this country and is of wide distribution, being found throughout the entire range of its hosts. Its normal host, on which it is most commonly found, is Ulmus americana.

The fungus is not ordinarily of much economic importance but may cause considerable injury to seedlings and young trees in nurseries by causing premature defoliation.

2. Unlike most of the Ascomycetes, the perithecial stage of the fungus begins its development in the living leaf early in the spring. The young perithecium develops in the palisade tissue beneath a subcuticular, black stroma.

3. An ascogonium is found in the young perithecium but there is no trichogyne.

4. An interascicular pseudoparenchyma is found present in the perithecium almost until the period of maturity.

5. In the process of ascospore expulsion an entire ascus enters the lower part of the ostiolar canal and the eight spores are apparently discharged simultaneously.

6. Since the ascospores could not be made to germinate in nutrient solutions or on artificial media, it would appear that some stimulus imparted by the living leaf of the host plant is required.

7. The fungus matures most rapidly during the winter on leaves which are neither too exposed nor in too damp a situation. When immersed in water or when in intimate contact with the soil, the fungus dies, and only the empty husks of the perithecia remain.

8. A conidial stage was found constantly associated with this ascigerous form. It is described as a new species, Gloeosporium ulmeum.

9. A new leaf-spot of the American elm, caused by Gloeosporium ulmicolum, another new species, is described. This species differs from the previously described one in the characters of the spot, and in the larger size of the spores.

10. Systremma Ulmi (Schleich.) Thiess. and Syd., causes a leaf spot of the European elms in Europe. Gnomonia ulmea has been very much confused with this fungus, and as a consequence, it has gotten into literature as occurring in this country. The probability is, however, that it does not occur in America at all. It is a member of the order Dothidiales, while Gnomonia ulmea belongs to the Sphaeriales.

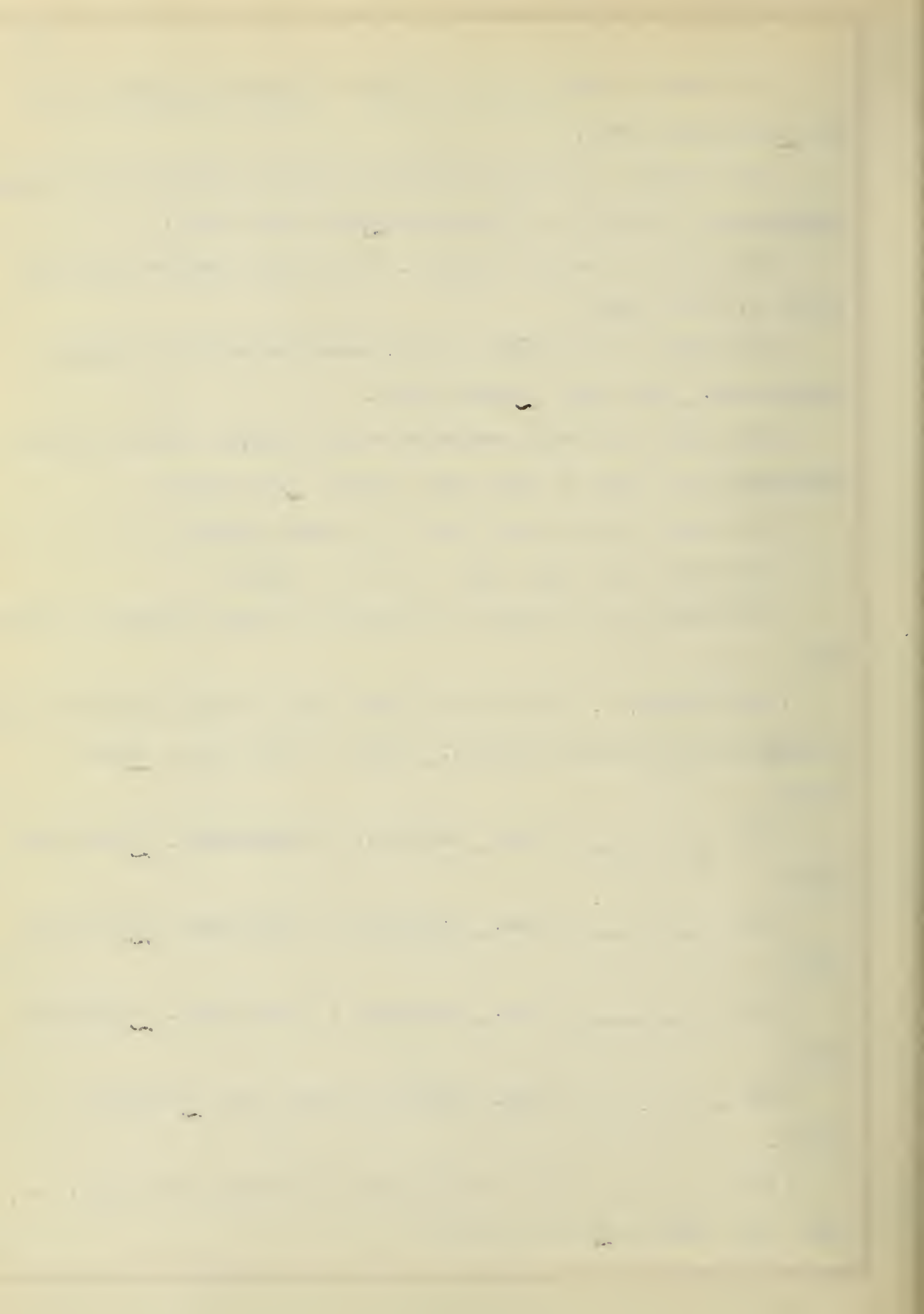
11. Other fungi producing leaf-spots on the elm are listed with a brief comment on each of the American forms.

12. Seven species of fungi are listed on the leaves of fossil elms.

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EXPLANATION OF PLATES.

PLATE I

Fig. 1. Two perithecia of Gnomonia ulmea in an almost mature condition, showing the interascicular pseudoparenchyma, and also the elongated beaks and the periphyses-lined ostiolar canal.

Fig. 2. Early stage in the development of the perithecium of Gnomonia ulmea, showing its position in the palisade layer. The subcuticular stroma above it has given rise to an acervulus of the imperfect form of the fungus, Gloeosporium ulmeum.

Fig. 3. Photograph of an elm leaf, showing one type of the Gnomonia spot. Note that there is no border of dead or browned tissue and that the stromata tend to coalesce.

Fig. 4. Photograph of an elm leaf, showing another type of the spot. The black stromata are surrounded by a border of dead tissue, light-brown in color.

Fig. 5. Same as Fig. 4 with the exception that the cuticle covering the stromata has begun to wear away, giving the spot a lighter, somewhat ashen appearance.

PLATE II

Fig. 6. Photograph of a leaf of the English elm, showing the leaf-spot caused by Systememna Ulmi. Note that each spot is but a single stroma, is much more definite in outline than that caused by the coalesced stromata of Gnomonia ulmea, and that they are raised much more above the surface of the leaf. Note also the wrinkled or papillate appearance of the stroma.

Fig. 7. Photograph of the Schweinitzian type specimen of Gnomonia ulmea.

Fig. 8. A perithecium of Gnomonia ulmea at the earliest stage in the development of the beak and ostiole. The dark portion of the perithecium represents the young asci which are just beginning their development. Note the pseudoparenchymatous contents of the perithecium.

Fig. 9. Photograph of an elm leaf, showing spots caused by Gloeosporium ulmicolum sp. nov. Note the manner in which the spots follow the veins. Compare with Figs. 3, 4, 5, 7, and 12 for differences from the spot caused by Gnomonia ulmea.

Fig. 10. Section through a stroma of Systremma Ulmi. It is subepidermal in origin. Note that there are no perithecial walls, and that the asci are borne in locules in the stroma which open on the upper side of the leaf.

Fig. 11. A single spot, Fig. 12a, enlarged ten diameters, showing the isolated character of the stromata of Gnomonia ulmea.

Fig. 12. Photograph of an elm leaf, showing the stromata of Gnomonia ulmea as they sometimes appear, widely separated in the spot and somewhat concentrically arranged.

Fig. 13. Very young stage in the development of the perithecium of Gnomonia ulmea, showing its pyriform shape at this stage, and its connection with the stroma.

PLATE III

Fig. 14. An acervulus of the conidial stage, Gloeosporium ulmeum sp. nov., formed above a young perithecium of the ascigerous stage, Gnomonia ulmea.

Fig. 15. Spores of Gloeosporium ulmeum. X 1800.

Fig. 16. Very young stage in the development of Gnomonia ulmea; a, sheathing hypha; b, ascogonium; c, "suspensor" or "infection thread"; d, vegetative hyphae which break through the stroma to the outer surface.

Fig. 17. Spores of Gloeosporium ulmicolum. X 1800

Fig. 18. Single acervulus of Gloeosporium stage of Gnomonia ulmea, showing manner of cracking to allow dispersal of spores. The hyphae about the acervulus are those of the basal stroma as viewed from above.

Fig. 19. Ascus and ascospores of Gnomonia ulmea. X 800.

VITA

The writer was born in Parke County, Indiana, September 25, 1890. He received his early education in the schools of that county, and graduated from Rockville High School in 1910. He then attended Wabash College, at Crawfordsville, Indiana, and graduated from that institution with the degree of A.B. in 1914. While in his third year at Wabash, in 1913, he was elected to Phi Beta Kappa.

In the fall of 1914 he accepted a position of Plant Physiological Assistant in Floriculture in the Illinois Agricultural Experiment Station, and registered in the Graduate School of the University of Illinois. In 1915 he was appointed Assistant in Botany in the University of Illinois, which position he retained until February of 1918, when he resigned for the purpose of entering the military service. In the fall of 1919 he was granted a Fellowship in Botany in the same University. He was elected to the University of Illinois chapter of Sigma Xi in 1917.

During the summers of 1917, 1918, and 1919 he was employed by the Bureau of Plant Industry as Field Assistant in White Pine Blister Rust Eradication.

His publications are:

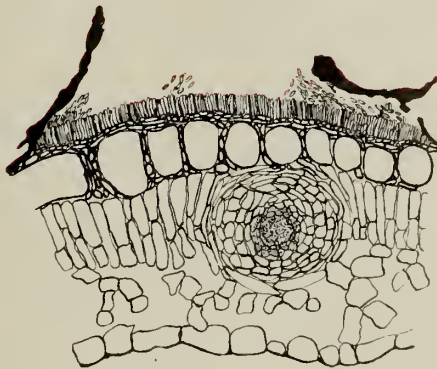
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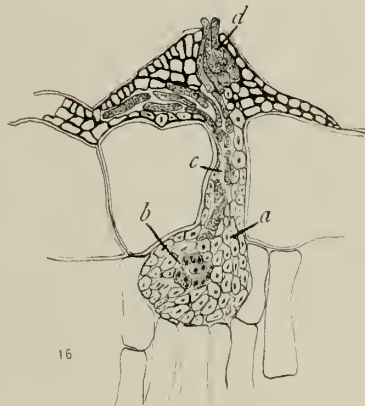
PLATE III



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PLATE I

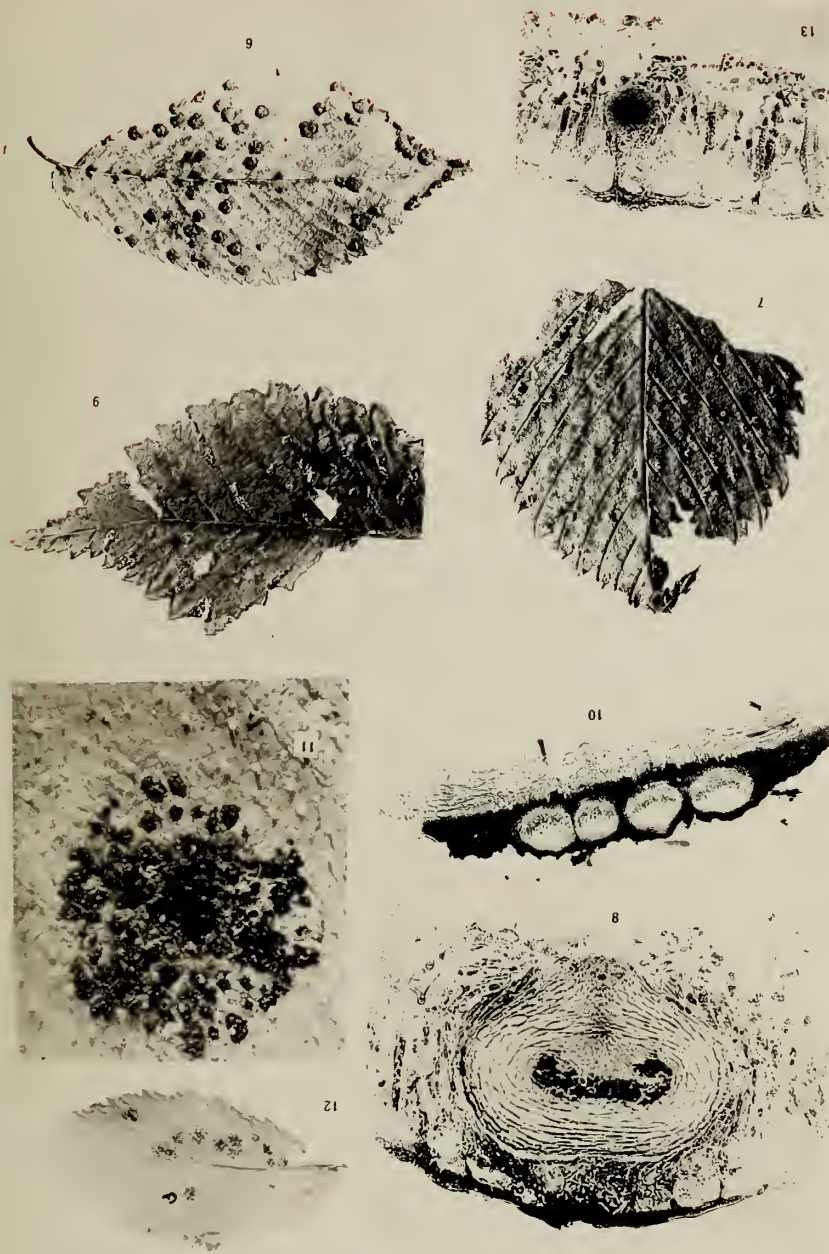
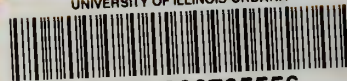


PLATE II

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